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Review

Why humans kill animals and why we cannot avoid it

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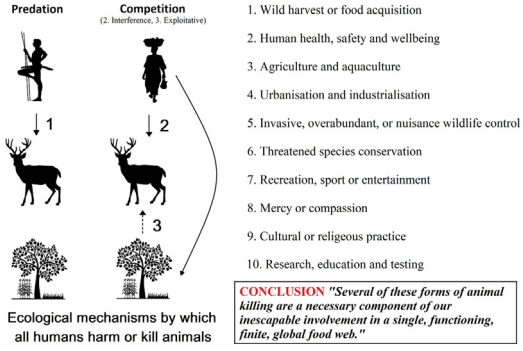
HIGHLIGHTS

- Killing animals is a ubiquitous human behaviour, but is increasingly controversial.
- We review 10 reasons humans kill animals, and ecologically contextualise them.
- Several forms of animal killing are a necessary component of human life on earth.
- Humans can modify some killing behaviours to improve the welfare of animals.
- A focus on welfare and sustainability can improve wild and domestic animal lives.

GRAPHICAL ABSTRACT

Overview of the ten reasons why humans kill animals, and why animal killing cannot be avoided.



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ABSTRACT

Killing animals has been a ubiquitous human behaviour throughout history, yet it is becoming increasingly controversial and criticised in some parts of contemporary human society. Here we review 10 primary reasons why humans kill animals, discuss the necessity (or not) of these forms of killing, and describe the global ecological context for human killing of animals. Humans historically and currently kill animals either directly or indirectly for the following reasons: (1) wild harvest or food acquisition, (2) human health and safety, (3) agriculture and aquaculture, (4) urbanisation and industrialisation, (5) invasive, overabundant or nuisance wildlife control, (6) threatened species conservation, (7) recreation, sport or entertainment, (8) mercy or compassion, (9) cultural and religious practice, and (10) research,

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Lethal control
Veganism

education and testing. While the necessity of some forms of animal killing is debatable and further depends on individual values, we emphasise that several of these forms of animal killing are a necessary component of our inescapable involvement in a single, functioning, finite, global food web. We conclude that humans (and all other animals) cannot live in a way that does not require animal killing either directly or indirectly, but humans can modify some of these killing behaviours in ways that improve the welfare of animals while they are alive, or to reduce animal suffering whenever they must be killed. We encourage a constructive dialogue that (1) accepts and permits human participation in one enormous global food web dependent on animal killing and (2) focuses on animal welfare and environmental sustainability. Doing so will improve the lives of both wild and domestic animals to a greater extent than efforts to avoid, prohibit or vilify human animal-killing behaviour.

Contents

1. Introduction . . . 2
2. Ten reasons humans kill animals . . . 3
2.1. Wild harvest, food acquisition . . . 3
2.2. Human health and safety . . . 3
2.3. Agriculture and aquaculture . . . 4
2.4. Urbanisation and industrialisation . . . 5
2.5. Invasive and overabundant native animal control . . . 6
2.6. Threatened species conservation . . . 6
2.7. Recreation, sport, entertainment . . . 7
2.8. Mercy or compassion . . . 7
2.9. Cultural and religious practice . . . 7
2.10. Research, education, and testing . . . 8
3. Animal killing behaviour in context . . . 9
4. Conclusions . . . 9
Article impact statement . . . 10
CRediT authorship contribution statement . . . 10
Data accessibility statement . . . 10
Funding statement . . . 10
Data availability . . . 10
Declaration of competing interest . . . 10
Acknowledgements . . . 10
References . . . 10

"*All stories, if continued far enough, end in death, and he is no true-story teller who would keep that from you.*"

[Death in the afternoon, Ernest Hemingway.]

1. Introduction

The killing of animals by humans has been a ubiquitous practice throughout history, and this pattern continues in the present age. Countless animals are killed daily either for direct consumption or indirectly through competition for resources, and the nutrients released through this process ultimately find their way back into the environment. Ecology textbooks refer to this as the 'food chain' or 'food web' (e.g. Caughley and Sinclair, 1994; Barbosa and Castellanos, 2005; Krebs, 2008; Molles, 2012). Animal killing by humans and animals is ecologically ubiquitous, yet some sectors of contemporary human society condemn, criticise or oppose animal killing by humans, attempting to prevent or minimise human involvement in the single, functioning, finite, global food web. Some more extreme adherents have even suggested that non-human predators might also be prevented from killing their prey (Bramble, 2021).

Criticism of animal killing comes in many forms. Modern hunter-gatherers and subsistence farmers are criticised for killing wild animals to feed themselves or to protect what little crops they can produce (Salerno et al., 2020). Livestock producers are criticised for raising and then killing domestic livestock and the wild predators and competitors of their livestock (Gruen and Jones, 2015; Leroy and Praet, 2017). Crop producers face the same criticism when they kill animals during tilling, during harvest, or when they protect their crops from being eaten by other animals (Singleton et al., 2007). Conservationists are criticised for killing exotic, invasive or overabundant animals to protect native biodiversity (Wallach et al., 2020b). Hunters are criticised for killing animals for food, sport or pleasure (Dickson et al., 2009). Cultures and religions are criticised for killing animals and disregarding animal suffering during various rituals (Velarde et al., 2014). Researchers, scientists and educators are also criticised for performing dissections or experimenting on and killing animals in laboratories (Badyal and Desai, 2014) or for field-testing ecological hypotheses related to animal killing (Yanco et al., 2019). This widespread criticism of killing animals occurs at all scales; it is directed towards global food industries such as the beef, dairy, pork, poultry and egg industries (Blanchette, 2018), government agencies at all levels, including, for example, the United States Department of Agriculture (Bergstrom et al., 2014) or Australian state and local governments (Probyn-Rapsey and Lennox, 2022), and is even targeted towards specific individuals including fishermen, recreational hunters, and wildlife scientists (e.g. Nelson et al., 2016).

Support for this criticism arises from a variety of perspectives. For example, some have argued that animal killing by humans is 'immoral', 'unethical', 'irreligious', 'unjust', 'unacceptable', or just plain 'wrong' (e.g. Abbate and Fischer, 2019). Others claim that animal killing ignores 'animal personhood' and that animals should have rights equal to humans, that animal 'abuse', 'violence' or 'murder' is unacceptable and criminal (Francione, 2009; Lennox, 2017; Wallach et al., 2020a), and that many people have held and still hold this belief (Singer, 1975; Regan, 1983). Many people also view the act of animal killing as 'cruel' or 'harmful' regardless of how it is accomplished or how instantaneous or painless it might actually be, and hence advocate for only non-lethal practices or complete cessation of animal killing, ostensibly to stop animal suffering (Wallach et al., 2018). Others have argued that animal killing does not resolve some of the issues it aims to address and is therefore unnecessary (e.g. it does not stop

depredation of livestock or does not contribute to the conservation of endangered species; Bergstrom et al., 2014). Others have further argued that killing animals is an inefficient way to obtain nutrition and that animal killing will be reduced by seeking our life-sustaining nutrients from lower trophic levels (i.e. vegetarianism or veganism; Katz, 1998; Middleton, 2009).

We authors agree with many of these perspectives and do not attempt to address or dispute each of these claims or worldviews here. Rather, as valid, strongly held, and important as these differing views might be, we consider them largely tangential to an ecological perspective on animal killing by humans and our undeniable role at the apex of the global food web. The philosophical, medical, veterinary, husbandry, and ecological literature is replete with robust debate on the acceptability of killing various animals in diverse circumstances, and it is clear that many people support or accept animal killing in one way or another while some others oppose it (e.g. Singer, 1975; Regan, 1983; Lehman, 1988; Miller, 2012; Deckers, 2016; Inglis, 2016; Nelson et al., 2016; Fischer, 2019; Lamey, 2019; Lecerf, 2020; Bobier and Allen, 2022a). However, we have observed that much of the 'for vs. against' multidisciplinary literature on this subject typically fails to put contemporary animal killing behaviour by humans into an evolutionary or ecological context, and an explanation for *why humans kill animals and why we cannot avoid it* has not been well articulated. Humans do not live independently of other species. We are an inescapable part of the global food web and our action, inaction, and mere presence on Earth has diverse consequences for animal life (Steffen et al., 2007). The disciplines of anthropology, archaeology, climate change, ecology, evolutionary biology, religious studies, philosophy and ethics, taxonomy and others implicitly attest to the interconnectedness of humans with other living organisms. We consider this a self-evident fact that should be understood by, or at least understandable for, most people.

Here we provide a brief overview of 10 primary reasons or categories of reasons why humans kill animals, or 10 primary forms of human animal-killing behaviour. Our broad definition of killing includes the intentional and unintentional actions and inactions of humans that directly or indirectly cause animal death, because any alternative or more restricted definition would knowingly omit important modes of human animal-killing behaviour (for further discussion, see McMahan, 2002; Singer, 2015). Animal killing is also multifunctional (Fischer et al., 2013). Thus, the 10 reasons we describe are non-exclusive and overlap in many cases, some may also be considered to fall into multiple categories, and our stated categories might also be reorganised in an alternative variety of acceptable ways. Though our rationale might apply to many types of animals, we focus our discussion on vertebrate animals which are almost universally recognised as being sentient. We argue that killing such animals is an unavoidable component of human life on Earth that might be reduced in some cases but is impossible to eliminate. We further argue that ethical debate over 'whether-or-not' to kill animals is unhelpful, and that a critical analysis of 'when' and 'how' to kill animals is much more relevant and consequential to improving animal lives. We encourage a future focus on animal welfare and the ecological sustainability of our animal killing behaviours, rather than focussing on binary ethical or philosophical issues like 'killing or not killing' or 'lethal or non-lethal' animal management. Although human dimensions – including worldviews, values, perceptions, attitudes, motivations, emotions and behaviours – are important drivers of why humans kill or do not kill animals, our primary aim was not to systematically review the sociological or psychological literature on anthopogenic reasonings for killing animals. Rather, our aim is to ecologically contextualise animal killing behaviour by humans, describe some of the implications of this for contemporary debates about animal ethics, and so provide a resource for those engaging in discussions about the permissibility and acceptability of killing animals. Our intended outcome is to redirect some of the philosophical and ethical debates away from intractable tensions between fundamentally different and somewhat theoretical worldviews towards applied issues that have a greater capacity to collectively improve the lives of both animals and people.

2. Ten reasons humans kill animals

2.1. Wild harvest, food acquisition

Many omnivorous and carnivorous predators, from insects to whales, hunt and kill wild animals for food. This behaviour is known as predation, and is a process integral to the proper functioning and maintenance of ecosystems (Molles, 2012; Smith and Smith, 2015). Predation can, and often does, cause great harm and suffering to the individual animal being killed (Allen et al., 2019). Some predators are specialists that target a narrow range of prey species, and others are generalists that target a wider range of prey species (Carbone et al., 1999, 2007). Humans, and their ancestors and relatives, are generalist, omnivorous mammals that have hunted, killed and harvested a wide variety of animals for approximately 2–4 million years (Faurby et al., 2020). Wild harvest is the most ancient form of predation by humans. Moreover, the evolution of humans' proportionately larger brain size is hypothesized to have occurred because of the fats and proteins acquired by eating animals, and therefore killing and eating animals was essential for the very emergence of humans (Mann, 2018; Leroy et al., 2023). Humans on or in the waters around all continents still harvest wild animals for food today, including people from developed and developing countries and those practicing traditional and contemporary lifestyles (e.g. Harris and Shilai, 1997; Dawson, 2018; El Bizri et al., 2020).

Many types of sentient and non-sentient animals are harvested, including echinoderms, molluscs, crustaceans, insects, fish, reptiles, birds and mammals (Heywood, 2013). Wild harvest of mammals, reptiles and birds is often characterised by low-volume or opportunistic hunting, such as the acquisition of bushmeat (Dawson, 2018; Haq et al., 2020). Other forms of high-volume or intensive harvesting are also practiced, such as the many fisheries in operation around the world (Pauly, 2016) or the commercial kangaroo (*Osphranter* spp., *Macropus* spp.) harvest in Australia (Pople and Grigg, 1999; Wilson and Edwards, 2019). Wild harvest of animals cannot be practiced without killing animals.

Wild harvest, predation, or directly killing animals for food can be avoided by adopting plant-based lifestyles (e.g. herbivory, or veganism), but doing so cannot avoid all the indirect forms of animal killing associated with such lifestyles (Hall and Tolhurst, 2007; Wills, 2019; Bobier, 2020; see also Sections 2.3 and 2.4). This type of indirect killing is known as competition, which can also lead to prolonged animal suffering, death and eventual extinction over time (e.g. Robin et al., 2009; Wilson and Edwards, 2019; see also Molles, 2012; Smith and Smith, 2015). Herbivory leads to competition-induced animal killing when humans eat plants that would otherwise be utilised by other animals, i.e. exploitative competition (Burrows et al., 2018). Competition-induced animal killing also occurs when fear effects behaviourally deprive animals of otherwise available resources (e.g. Clinchy et al., 2016; Suraci et al., 2019), i.e. interference competition. Hence, the wild harvest of both animals and plants results in animal killing; the primary difference is that one is direct killing and the other is indirect killing (Fig. 1). Human carnivory and herbivory are forms of wild harvest that are ubiquitous across trophic levels, ecosystems and epochs (Barbosa and Castellanos, 2005; Molles, 2012; Smith and Smith, 2015). All forms of wild harvest cause harm to animals, and there are no viable alternatives to these forms of animal killing if we are to continue feeding the approximately 8,000,000,000 humans on the planet (Hampton et al., 2021). Directly killing animals for food can often be done in ways that cause no or negligible amounts of pain or harm (Sharp and Saunders, 2011; Hampton et al., 2015a; Fig. 2). When done in these ways it can give animals a more humane or painless death than the alternatives they would otherwise experience from large-scale plant- or animal-based agriculture (Demetriou and Fischer, 2018) or through natural causes such as disease, starvation, or intraspecific fighting.

2.2. Human health and safety

Killing animals in self-defence or to protect human health and safety is also one of the most ancient forms of animal killing by humans. It is done

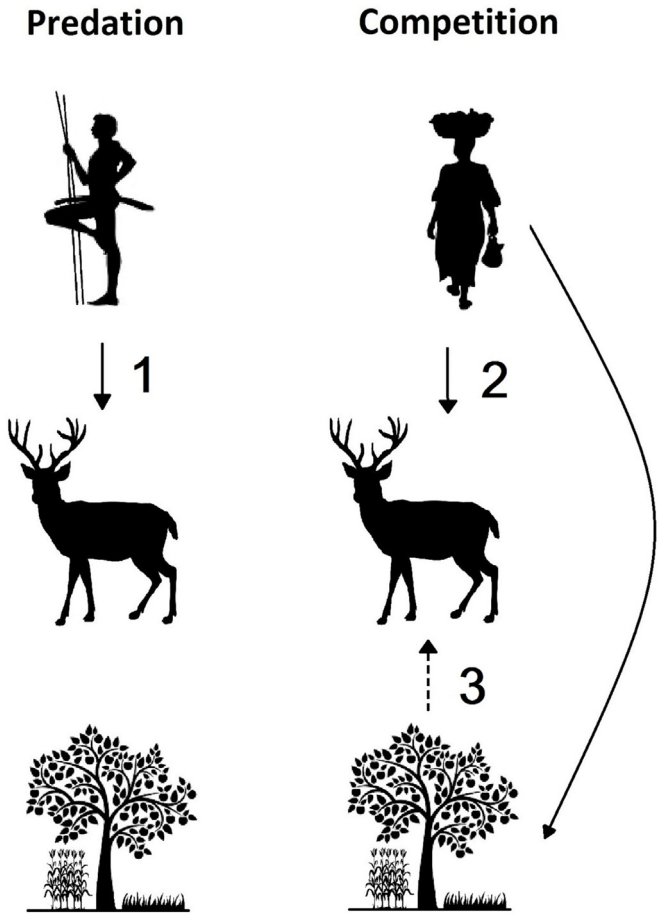

Fig. 1. Three ecological mechanisms of animal killing behaviour by humans, showing (1) predation (e.g. carnivory or meat-based diets), (2) interference competition (e.g. when animals are behaviourally deprived of access to shared resources, or fear effects), and (3) exploitative competition (e.g. herbivory or plant-based diets, or consumption of shared resources). Solid lines = direct effects, broken lines = indirect effects.

proactively when an animal is killed to prevent a possible threat or reactively to eliminate a present threat. Examples of proactively killing animals for human health and safety reasons include killing large carnivores (e.g. lions *Panthera leo*, saltwater crocodiles *Crocodylus porosus*, or great white sharks *Carcharodon carcharias*) in the vicinity of human settlements (e.g. Ferretti et al., 2015), or controlling populations of smaller mammals (such as racoons *Procyon lotor*, feral dogs *Canis familiaris*, or black rats *Rattus rattus*) to prevent the spread of zoonoses including rabies or leptospirosis (Witmer and Proulx, 2010; Rosatte, 2013). Reactive killing for human health and safety reasons occurs when any animal attempts to harm or kill a human and the humans kill the animal in self-defence. Examples include killing Asian elephants *Elephas maximus* (Fernando, 2015), cougars *Puma concolor* (Thornton and Quinn, 2009), or eastern brown snakes *Pseudonaja textilis* (Whitaker and Shine, 2000) that had attacked humans. Killing animals for traditional medicinal use is another expression of killing for human health reasons practiced in many parts of the world (Loveridge et al., 2017; Haq et al., 2020), and the raising and killing of genetically-modified pigs *Sus scrofa* to provide a source of replacement organs for xenotransplantation into humans represents an emerging form of killing animals for human health reasons (Montgomery et al., 2022). Proactive and reactive forms of animal killing (such as control of rodents in impoverished neighbourhoods) may also improve human mental health and wellbeing by reducing anxiety over both food security and disease risk (e.g. Shah et al., 2018; Byers et al., 2019).

In many, or perhaps most, cases there may be less harmful or even non-lethal ways to eliminate human health and safety risks from animals, which might eliminate the need to kill animals, especially contemporary proactive forms of animal killing (see Sections 2.3 and 2.5). This could include vaccinating animals (Gilbert et al., 2018a) and humans (Kessels et al., 2017) against zoonoses, installing animal exclusion fencing around human communities (Yamazaki and Bwalya, 1999), sealing buildings and grain silos to exclude grain-destroying birds and rodents (Mullen and Pedersen, 2000), or managing risk-enhancing human behaviours (Penteriani et al., 2016). It might also be possible to reduce the need for reactive forms of animal killing by increasing tolerance of perceived threats, or by taking appropriate measures to prevent an incident or animal attack from arising, including avoidance of areas with high densities of large carnivores or other dangerous animals (Gurung et al., 2008; Fukuda et al., 2014; Behrendorff, 2021). Such non-lethal practices might also include maintaining strong biosecurity systems to prevent zoonotic diseases or their animal vectors from invading new areas (see Section 2.5), chasing or relocating dangerous animals away from vulnerable humans (Appleby et al., 2017), or adoption of plant-based traditional medicines or modern manufactured medicines rather than animal-based traditional medicines where culturally appropriate. Refraining from killing animals to protect human health and safety might be possible for some humans to avoid, particularly those in affluent circumstances; but because of human inequality and poverty across much of the world, refraining from this form of animal killing will be largely impossible at broader societal scales without compromising human welfare, ignoring cultural sensitivities, and losing human lives.

2.3. Agriculture and aquaculture

Agriculture and aquaculture are associated with the most globally prevalent forms of animal killing (e.g. Gilbert et al., 2018b). Agriculture has been practiced by humans for at least 11,000 years and enabled humans to establish themselves as the dominant vertebrate on Earth (Diamond, 1999). Agriculture includes the production and protection of both plants and animals in both small (i.e. subsistence farming) and large (i.e. commercial farming) quantities (Hampton et al., 2021). Agriculture and aquaculture are forms of optimal foraging behaviour, whereby animals and humans obtain food resources in ways that minimise risk and optimize energy expenditure (Brown et al., 1999). These practices are also analogous to caching behaviour or food storage given that a live animal can convert biomass inedible to humans into edible protein that can be consumed later at times of seasonal shortage of other plant-based foods. Humans farm and kill a wide variety of mammals (e.g. domestic cattle *Bos taurus*, sheep *Ovis aries*, goats *Capra hircus* and pigs), birds (e.g. domestic chickens *Gallus gallus*, ducks *Anas platyrhynchos*, geese *Anser anser*, turkeys *Meleagris gallopavo*, pigeons *Columba livia* and ostriches *Struthio camelus*), fish (e.g. Atlantic salmon *Salmo salar*, common carp *Cyprinus carpio*, and bluefin tuna *Thunnus thynnus*) and other animals (e.g. prawns, oysters, or turtles such as *Chelodina rugosa*) for their meat. Animals are also farmed and killed for other reasons, such as obtaining milk and eggs (e.g. killing male dairy cattle or male egg-breed chickens) or feathers, fur, skins or leather (e.g. ostriches, crocodilians, or American mink *Neovison vison*).

Beyond the direct killing and use of farmed animals for food or fibre, wild predators and competitors of farmed animals and plants negatively affect the production of farmed species in many cases and are also intentionally killed to mitigate the agricultural production losses they would otherwise cause (Allen and West, 2013; Wills, 2019; Cabral de Mel et al., 2022). Examples include the killing of canids, felids or mustelids to mitigate their predation on farmed animals (e.g. Thorn et al., 2013), or the killing of ungulates, macropods, birds or rodents to mitigate their competition for farmed plants (e.g. Flores, 2016; Clark et al., 2018; du Plessis et al., 2018; Somers et al., 2018). Other examples include killing infected domestic and wild animals to stem disease outbreaks that could harm and kill vast numbers of livestock and wild animals (e.g. biosecurity activities). Such diseases include foot-and-mouth disease, rabies, tuberculosis, anthrax, avian influenza, African swine fever, and many others (e.g. Griffin and O'Reilly, 2003; Wolfe et al., 2004; Rosatte, 2013; Nugent et al., 2015; Arruda et al., 2020). Indirect killing occurs when non-target animals die from accidental

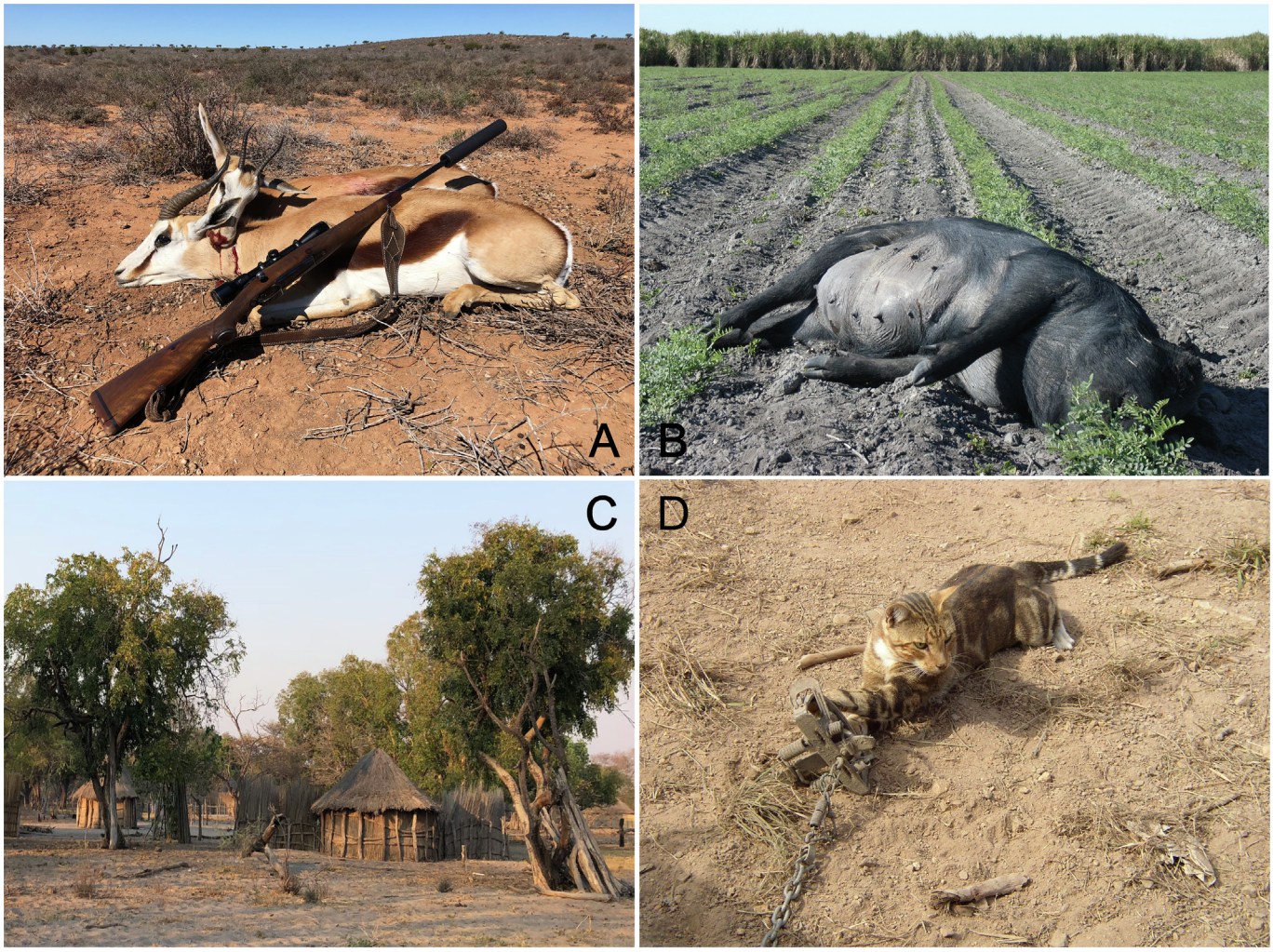

Fig. 2. Examples of direct and indirect animal killing by humans, showing: (A) two springbok *Antidorcas marsupialis* wild-harvested for meat in South Africa (Section 2.1); (B) land clearing for peanut *Arachis hypogaea* and sugar cane *Saccharum* spp. crops in Australia, including a feral pig *Sus scrofa* shot to alleviate damage to the crops (Section 2.3); (C) small-scale urbanisation illustrated by a group of rondevals under trees in Botswana (Section 2.4); and (D) a feral cat *Felis catus* trapped in Australia to protect threatened fauna from cat predation (Sections 2.5 and 2.6). Photo credits: Benjamin Allen.

poisoning associated with use of the drugs, pesticides and herbicides used to protect animals and plants (e.g. Stutterheim, 1982; Oaks et al., 2004) or as bycatch in traps intended for damage-causing animals.

Although it is not often viewed as a source of animal killing, the establishment and harvesting of crops (e.g. land clearing, tilling) required and still requires the direct and indirect killing and displacement of animals (i.e. interference competition) at enormous scales, as does the protection of crops following establishment (Wills, 2019; Hampton et al., 2021; Fig. 2; see also Section 2.4). For example, red-billed quelea (*Quelea quelea*) are killed in their millions to protect grain crops (McWilliam and Cheke, 2004). Demand for soybeans (*Glycine* max) and palm oil (*Elaeis guineensis*) has also been a major driver of deforestation in South America and Southeast Asia, causing the displacement and death of innumerable animals through the destruction of the natural habitat they relied on (Weinhold et al., 2013; Frey et al., 2018). Many, but not all of such crops or their by-products might also be used for industrial non-food purposes like biofuels or livestock feeds (Ray et al., 2022). Approximately one-third of crops grown across the world also require animal manure for fertilisation, which inherently requires livestock farming to accumulate manure for later dispersal, causing consequent displacement and death of other animals (e.g. Mkhabela, 2006).

Whether animals are killed to be eaten or worn, or because almost all animals have been eliminated from land where we now grow biofuel crops or food crops for ourselves or our livestock (Chaudhary et al., 2016; see also https://ourworldindata.org/soy), animal killing is an indisputable and unavoidable component of both the plant and animal food production systems that support human life (Hampton et al., 2021; Croney and Swanson, 2023). Engaging in animal and plant agriculture and aquaculture in this way enables a greater amount of food to be obtained for humans than would otherwise be attainable through wild harvest (Section 2.1). It is, of course, possible to produce livestock and crops in ways that minimise both the direct and indirect impacts on wild animal lives (e.g. du Plessis et al., 2018; Allen and Hampton, 2020), but generating food on such large scales to feed a large and growing global human population is impossible without killing animals (Allen and West, 2013; Tank and Thiele, 2019). Killing animals for agriculture is a critical human food security endeavour (e.g. Singleton et al., 2010; Salerno et al., 2020; Croney and Swanson, 2023), and many humans will die if humans do not kill animals to produce and protect animal-based and plant-based agriculture and aquaculture.

2.4. Urbanisation and industrialisation

Perhaps the most universal form of animal killing occurs when humans construct houses, factories, mines, power stations, roads, railways, and other industries and infrastructure needed to support sedentary human populations. In ecological terms, urbanisation might be better thought of as mass, irreversible habitat destruction that has resulted in some of the

highest rates of decline and local extinction of a range of fauna worldwide (Czech et al., 2000; McKinney, 2002; Skead, 2007). Urbanisation thus kills animals in ways similar to intensive agriculture (Section 2.3), which is intrinsically linked to feeding a rapidly urbanising human population. Furthermore, because urban areas are typically situated in places that were once biodiversity hotspots (Cincotta et al., 2000), the impacts on flora and fauna are more severe for urbanisation than for most other human activities.

Urbanisation represents competition for the critical resource of space and results in the killing and expulsion of countless other animals whenever it occurs at either large or small scales. For example, koalas (*Phascolarctos cinereus*) are arboreal dietary specialists distributed along the entire east coast of Australia, where most of the Australian human population lives in multiple cities. Within just a 10 year period, the national conservation status of koalas has deteriorated from being *unlisted*, to listed as *vulnerable* in 2012, and then to *endangered* in 2022, almost exclusively through the ongoing direct and indirect effects of urbanisation – vehicle collisions and tree clearing, or removing both the food and refuge of this iconic species (Dique et al., 2003; McAlpine et al., 2015). Though far smaller in scale, the establishment of rondavels under trees in the Okavango Delta of Botswana similarly displaces the wild animals that would otherwise live there (Fig. 2). Thus, every living human on the planet contributes to the displacement and death of animals in this way and/or has and is benefitting from the proceeds of such animal killing in the past (Sections 2.1–2.3 and 2.5–2.10).

Continued animal killing through urbanisation seems inevitable so long as global human population growth remains positive and the current trend of migration towards urban nodes continues. Directly killing medium- and large-sized animals may be avoidable when construction is undertaken carefully and affected individual animals are captured and translocated. However, the subsequent displacement and indirect forms of animal killing (e.g. lack of food, exposure to predation, diseases or pollutants) associated with urbanisation are largely unavoidable. The number of animals killed in this way may be reduced to some degree when urbanisation is directed upwards and not outwards or when water and waste are recycled sustainably. However, increasing human populations will still place ever increasing demands on natural resources and the associated industry and infrastructure required to support sedentary populations, which are almost always permanent.

2.5. Invasive and overabundant native animal control

Killing exotic, non-native, extralimital, or overabundant native animals is practiced widely. However, the motivation for this type of killing is distinct from other forms of animal killing. Animals might be killed by humans simply because they are exotic or 'not from here' (van Eeden et al., 2020), but they are usually killed because their invasive characteristics and traits (Elton, 1958) raise concern that they will cause subsequent issues that will require further and otherwise avoidable animal killing (Fleming et al., 2017; Callen et al., 2020). These concerns include the protection of human health and safety (Section 2.2), agricultural production (Section 2.3), threatened species protection (Section 2.6), or the prevention of ecosystem collapse or shifts characterised by the mass killing and loss of many local animals. Many invasive and overabundant animals create real and perceived undesirable impacts on the environment, human economies, and on social or cultural values (e.g. Witmer and Proulx, 2010; Castorani and Hovel, 2015; Doherty et al., 2016; Fleming et al., 2017; Diagne et al., 2021). These impacts include the harm, killing and death of relatively large numbers of other animals that could otherwise be alleviated and avoided by killing relatively small numbers of invasive and overabundant native animals (e.g. Heriot et al., 2019; Allen and Hampton, 2020; Raine et al., 2020). Killing invasive animals typically aims to prevent, for example, any potential negative impacts on agriculture, native species, wilderness areas, or human health.

Directly (Russell et al., 2016) and indirectly (Zavaleta et al., 2001) killing invasive and overabundant species may be avoidable, but doing so will often yield unavoidable adverse consequences for both humans and animals. Though it may sometimes be possible to undertake invasive animal control in ostensibly non-lethal ways, such as trap-neuter-release or translocation, these practices are often ineffective and typically cause greater harm to animals than simply killing them (Sharp and Saunders, 2011; Hampton et al., 2015b; Hampton et al., 2017). Attempted 'non-lethal' exclusion of invasive animals by creating landscapes of fear can create serious animal welfare issues, in addition to indirect killing (Brown et al., 1999; Creel, 2018; Allen et al., 2019). So, while restoring ecosystems through restoration of native carnivores and herbivores might 'naturally' eliminate invasive and overabundant animals (Soulé and Noss, 1998; Funk et al., 2008), this does not evade animal killing given subsequent predation and competition; it merely outsources animal killing from humans to animals or other ecological processes (e.g. predation, starvation, disease). Sometimes it is simply impossible to remove all invading animals without killing at least some of them (Fleming and Ballard, 2019). Humans do not need to kill or exclude invasive or overabundant invasive animals like they need to eat or protect themselves (see Sections 2.1–2.3), but past experience indicates that allowing invasive and overabundant native animal populations to grow unchecked usually results in ecosystem degradation, including widespread harm and death to many other animals (Hayward et al., 2019; Wilson and Edwards, 2019; Callen et al., 2020; Diagne et al., 2021) and to the agricultural products that humans rely on for food (Paini et al., 2016; Section 2.3).

2.6. Threatened species conservation

Killing one animal to save another more threatened or less abundant animal is largely an altruistic act, though humans might derive some aesthetic benefit from retaining only native species in a given location (Section 2.5). Killing animals (either native or non-native) to protect threatened species is also common across continents. Non-native examples include killing feral cats *Felis catus*, brushtail possums *Trichosurus vulpecula*, or stoats *Mustela erminia* to protect small mammals and ground-nesting birds in Australia and New Zealand (Morgan et al., 2006; Read, 2019; Fig. 2), killing grey squirrels *Sciurus carolinensis* to protect red squirrels *Sciurus vulgaris* in Europe (Bertolino and Genovesi, 2003), killing camels *Camelus dromedarius* to protect the water sources used by native animals in Australia (Knight, 2018), or killing rodents to protect seabirds or endangered endemic rodents on oceanic islands (Raine et al., 2020; Jones et al., 2021). Native examples include killing dingoes *Canis familiaris* to protect rufous hare-wallabies *Lagorchestes hirsutus* in Australia (Gibson et al., 1995), or killing barred owls *Strix varia* to protect spotted owls *Strix occidentalis* in North America (Livezey, 2010). Many examples of this form of killing involve killing predators to alleviate their impacts on prey. Additional examples include killing common herbivores to alleviate competition with threatened herbivores (Sharp et al., 1999) or killing herbivores to reduce their impacts on threatened plants (McAlpine et al., 2015; Drijfhout et al., 2020; Allen et al., 2021). Population control (i.e. killing) of various carnivore and herbivore species is also required in smaller protected areas to ensure that overutilization of resources (either plants or animals) by one or more species does not cause the death and decline of others (Miller and Funston, 2014).

This type of animal killing may be a necessary (Fleming and Ballard, 2019), temporary solution when abundant vertebrates pose an immediate threat to the survival of a rare species (Goodrich and Buskirk, 1995) given that killing relatively few animals in the short term can reduce the overall numbers of animals killed in the long term (Warburton et al., 2012; Allen and Hampton, 2020). However, the repeated killing of common animals to save endangered ones may produce several adverse outcomes, including the high cost of population control, ecosystem changes that favour increases of other harmful species, or increases of diseases harmful to the endangered species (Goodrich and Buskirk, 1995). Habitat rehabilitation and restoration programs may be better solutions to problems caused by abundant native animal species because community and ecosystem degradation are the ultimate causal factors responsible for some species becoming rare and others becoming abundant (e.g. Allen, 2011; Stobo-Wilson et al., 2020). These solutions are long-term,

biologically sound, and involve little direct human intervention into ecosystem processes (Goodrich and Buskirk, 1995; Proulx and Powell, 2016). Thus, humans do not need to kill animals to save other animals, but abstaining would knowingly magnify the number of individual animals killed and condemn entire species to extinction in some cases.

2.7. Recreation, sport, entertainment

Recreational hunting and fishing, or killing animals for sport or entertainment, is a particularly contentious form of animal killing by humans (Cohen, 2014; Darimont et al., 2017; Batavia et al., 2019; see also Nelson et al., 2016). This practice is also distinguished from other types of animal killing by its motivation. For example, recreational hunting and fishing do not always result in consuming the animal, but when it does, this behaviour might be better classified as wild harvest (Section 2.1). Here, we define recreational killing as being purely for entertainment, sport, or pleasure, including collecting trophies, achieving personal goals (e.g. catching a large fish), facilitating gambling, or keeping pet animals.

This type of animal killing by humans evolved out of necessity to acquire food and protect life or property (see Sections 2.1–2.4), and the behaviour further developed as a rite of passage, or a demonstration of personal skill or work ethic also associated with mate acquisition (Hawkes and Bliege Bird, 2002; Darimont et al., 2017). However, continued cultural evolution in many human societies has meant that recreational hunting is now undertaken as a largely symbolic gesture or pleasurable use of time. Alternatively, recreational hunting might be interpreted as a righteously defiant (i.e. defiant of moral arguments that discourage recreational hunting) ritual resembling animal sacrifice in the religious sphere (Cohen, 2014; see also Section 2.9).

There are countless examples of recreational killing by humans – virtually any animal with horns, large teeth or tusks, or attractive fur or feathers has been, or is still, hunted for sport. High-profile examples include red fox hunting in England (Marvin, 2000) or lion hunting in southern Africa (Macdonald et al., 2016). Lesser known examples include live-baiting with rabbits *Oryctolagus cuniculus* to train greyhound dogs (Hampton et al., 2020). Many wild animals are also killed to feed the billions of pet animals (i.e. cats and dogs) kept by humans for pleasure. For example, 13.5 % of the total 39 million tonnes of wild caught fish is used to support the pet food industry (De Silva and Turchini, 2008). Cock, dog and bull fighting are other forms of recreational animal killing (e.g. María et al., 2017); and in the case of bull fighting, is also a legally-protected cultural heritage activity (Section 2.9). Death of the animal is the intended goal or at least an unavoidable outcome of recreational killing in many cases (e.g. to acquire a trophy). Yet some forms of such recreation do not require killing, including the catch-and-release practices common to fishermen (Cooke and Schramm, 2007) or the type of no-kill trophy hunting proposed by Cove (2019). These practices cause some harm to animals, which might inadvertently die on occasion, but they do not necessarily demand animal killing. Such non-consumptive activities still require skills used in recreational hunting, such as wildlife photography, bird watching, or snow tracking, and might therefore be as personally rewarding as killing the animal in some cases (Cove, 2019). Many forms of recreational killing may be avoidable. However, without alternative revenue streams, cessation of these practices will indirectly result in the death of many animals given that wildlife conservation efforts in many parts of the world are directly funded through recreational killing activities (e.g. Lindsey et al., 2007; Heffelfinger et al., 2013; Baxter et al., 2018; Clark et al., 2023). Recreational hunting may also contribute to wildlife conservation through the suppression of overabundant game species (Williams et al., 2013; Gortázar and Fernandez-de-Simon, 2022; Section 2.5).

2.8. Mercy or compassion

Humans frequently kill animals out of mercy or for compassionate reasons. For example, humans will often have a beloved pet dog or cat killed by a veterinarian (i.e. euthanized) to avoid continued suffering when the pet becomes old or ill. Various wildlife species injured in predation attempts, road collisions or other accidents are also euthanized to prevent the inevitable suffering and likely death that will occur if the animal is left in the vain hope it will later recover (e.g. Allen et al., 2015). Euthanasia may also be appropriate for wildlife casualties that are a danger to other animals or humans. In some circumstances involving a flock, herd or group problem (i.e. a disease outbreak), euthanasia of a small number of ill animals may also be required to provide a diagnosis allowing appropriate treatment of the remainder of the flock, herd or group. Healthy animals in zoos or fenced reserves might also be killed because they are surplus to requirements (e.g. genetically similar individuals might lead to inbreeding and compromise breeding programs), or to prevent them from being killed by other animals or ecological processes given a lack of space to accommodate them (Miller and Funston, 2014; see also Section 2.6). A variety of other, more nuanced reasons might further necessitate mercy killing, especially in veterinary care settings (e.g. DES, 2013, pp. 16–17).

Unlike wild harvest (Section 2.1), agriculture (Section 2.3) or urbanisation (Section 2.4), where killing is unavoidable, compassionate killing or mercy killing is easily avoidable by 'doing nothing' (Bobier and Allen, 2022b). Debilitated animals might even be kept intentionally alive with palliative care to facilitate the generation of induced pluripotent stem cells (iPSCs), which are useful for developing therapeutic applications for captive animals that suffer from degenerative diseases or for preserving the genomes of individuals for later use in genetic rescue efforts (Ben-Nun et al., 2011; Comizzoli, 2017; Honda et al., 2017; see also Section 2.6). However, suffering animals with a poor prognosis for survival are typically euthanized rather than left to die more slowly because inaction causes preventable harm to animals, and failure to kill the animal can be a punishable breach of animal welfare law in some countries (DES, 2013; Rioja-Lang et al., 2020). This interplay between animal ethics and animal welfare means that in cases of mercy killing, humans must choose to shorten suffering and kill the animal or avoid killing the animal and prolong suffering (Bobier and Allen, 2022b). The moral acceptability of mercy or compassionate killing is grounded in the understanding that killing the animal results in less harm than allowing the animal to live – a 'good death' is seen as a more desirable alternative to a 'bad life' when a 'good life' is not possible (Nobis, 2019).

2.9. Cultural and religious practice

Buddhism, Islam, Hinduism, Judaism, and Christianity – indeed almost all the world's major religions and cultures permit the killing of various animals for the purpose of eating meat (Sections 2.1 and 2.3). Cultural practices around the world also sanction animal killing for non-consumptive purposes, including religious animal sacrifices to a deity or god (Zoethout, 2013). Animals sacrificed to a deity may or may not be subsequently eaten.

Although 'life is dear to all' in Buddhism, where the precept 'one should not kill nor cause others to kill' is sometimes applied through strict vegetarianism (Buddharakkhita, 1985), meat-eating is still commonplace in most Buddhist societies. Other branches of Buddhism permit what might be described as 'scavenging' when the meat is available or offered rather than intentionally killed (Barstow, 2019). The sacrifice of sheep, goats, cows, camels and sometimes yaks *Bos grunniens* and banteng *Bos javanicus* is commonly practiced in Islamic communities around the world in association with the celebration of the Eid al-Adha (i.e. 'feast of sacrifice', 'great feast', 'sacrifice feast', or 'goat feast') during the Hajj or pilgrimage (Roy, 2005). In Indonesia alone, approximately 800,000 goats were sacrificed during the festival in 2014 (Anon., 2015). About 2.5 million sheep, cows and goats are sacrificed during this festival in Turkey each year, and about 10 million in Pakistan (Zaidi and Chen, 2011). Muslims also perform animal sacrifices on other religious occasions (Roy, 2005). Animal sacrifice is also widespread in polytheistic Hindu cultures, where various traditions sacrifice animals to a variety of deities, especially in India and Nepal, where mainly goats, buffaloes *Bubalus bubalis* and chickens are killed (Raj, 2004). Pacific Island cultures also sacrifice animals. For example,

chickens or goats are sacrificed to wanamo (a half-man half-dog spirit that protects the forest) in the Bundi region of Papua New Guinea to secure safe passage through the forest for people that do not belong to the local indigenous tribe (B. Allen, personal observations). Animal sacrifice is also common in many African cultures, such as the Isese or Yoruba religion found in West Africa and the Afro-American religions of the Caribbean (e.g. Ozioma and Chinwe, 2019).

Animal sacrifices were practiced extensively in ancient Jewish, Christian and other monotheistic cultures of the Near East and beyond in Europe and North Africa. For ancient Jews and Christians, the practice was originally designed to teach about the future sacrifice of the Messiah or Jesus Christ, which then understandably ceased following Jesus' crucifixion circa 33 CE when the sacrament or communion (i.e. broken bread and wine) was instead instituted to remember Jesus' sacrifice. A small number of contemporary Christian denominations in Europe, northern Africa, and Mexico still practice a restricted form of animal sacrifice today, killing sheep, chickens or pigeons (e.g. Shepard, 2011; Siekierski, 2013). With a history deeply rooted in Judeo-Christian values (Shapiro, 2016), most contemporary western cultures do not exhibit animal sacrifice traditions. Nevertheless, landmark cases brought to the Supreme Court of the United States of America (USA) may permit the practice of ritual animal killing in the USA under their constitutional provision of religious freedom (Holzer, 1995) – a freedom not supported in Europe (Zoethout, 2013).

These examples illustrate the widespread use of animal sacrifice in ancient and modern cultures in all areas of the world and the diverse expression of the practice across different communities. However, animals are also ritually killed for reasons other than worshipping a deity (Ruel, 1990). For many, the animal sacrifice is itself constitutive of interspecies kin relations, and the spectacular act of violence at the heart of the sacrifice (e.g. the beheading of the sacrificial animal) is crucial to the constitution of kin solidarity between the human sacrificer and animal victim (Govindrajan, 2015). Not all cultural killing of animals is for religious reasons or involves sacrifice (McCorquodale, 1997). Feasts, where special foods such as 'the fatted calf' or unusual quantities of food are served, can be for socio-political purposes, without sacrifice but accompanied by rituals associated with the killing of the animals to serve at the feast (Dietler, 2001). Exotic cooked flesh can be used to welcome or impress guests, establish or maintain prestige, power or face, or accompany initiations into a society (Hayden, 2014). Gatherings of people to benefit from super-abundances of food, such as migratory or seasonally abundant animals (e.g. fish migrations; see also Section 2.1), are often culturally linked to phenological signals and associated ceremonies. For example, ceremonies of food availability, harvesting and use prescriptions were, and are, ritually enacted and celebrated by First Nations peoples in Canada and Australia (e.g. Lantz and Turner, 2003; Fordham et al., 2006) and bat-harvesting festivals are annually celebrated in north-east India (Low et al., 2021).

It might be argued that humans do not need to kill animals for purely cultural or religious reasons, and there are indeed some noteworthy examples of rapid cultural change to avoid animal killing (e.g. Naude et al., 2020; Sibanda et al., 2022). However, we suspect that many people will still feel so deeply about the issue that it could be described as a *need*, and denigration or suppression of those religious and cultural needs might be considered bigotry, epistemicide or cultural imperialism. Expression of the very idea that proper or more developed religions are superior to primitive barbaric religions is typically divisive, racist, and deeply rooted in colonialism (van der Veer, 2011; Tayob, 2022). Though the practice of animal sacrifice will remain subject to criticism by some people, it is likely to continue except where it is prohibited by law (e.g. Deb, 2019). Thus, many cultural and religious practices will continue to require the killing of animals and cannot be easily substituted with practices that do not require animal killing.

2.10. Research, education, and testing

Killing animals for research, education and testing purposes is treated separately here because of its unique reasoning. However, it might also be thought of as an extension to, or component of, many of the other preceding reasons for animal killing by humans (Sections 2.1–2.9) given that animal research is often conducted to support our understanding and implementation of those other reasons. Animals are used in scientific and medical research and education to understand a whole range of questions relating to how human and animal bodies work, what causes diseases in humans and animals, or attempts to develop therapeutic and cosmetic treatments that are safe and effective (Gauthier and Griffin, 2005). Many, if not most, of the remarkable innovations in our medical understanding and treatment of contemporary human maladies have been at least partly derived from research using animals (Garattini, 1990; Bishop and Nolen, 2001). The use of animals for research, education and testing is typically highly regulated to ensure such use is justified on ethical and welfare grounds.

Millions of animals are used each year in research and education (e.g. dissection, vivisection, and veterinary training). However, adherence to Russell and Burch's (1959) '3 Rs' principle is now a requirement of most, if not all, legislated and self-regulated national surveillance systems to ensure this use of animals is justified (e.g. SABS, 2008; NHMRC, 2013). The *replacement* of animals in research has occurred mainly through improvements in techniques, which enable scientists to look for mechanisms of action at the cellular and molecular levels rather than using a 'whole animal' approach (Gauthier and Griffin, 2005). Most national systems of animal research oversight also require *reductions* in the use of animals where possible, directing that animals should only be used when no other method is available to meet the scientific aims of the study. The *refinement* of techniques has resulted in less harm and fewer animal deaths in experimental procedures. Refinement not only improves the lives of research animals, but it can also improve the quality of the science (NHMRC, 2013).

One obvious way to improve animal welfare while using animals for research or education purposes is to create an environment that meets the animals' specific needs. To this end, Mellor and Reid (1994) developed the '5 domains model' (originally based on the United Kingdom Farm Animal Welfare Council's '5 freedoms') to assist in identifying welfare impacts under the following domains: nutrition, environment, health, behaviour, and mental state. While the implementation of Russell and Burch's '3 Rs' principle and Mellor and Reid's '5 domains' model have contributed enormously to the responsible use of animals in scientific research, the use and killing of animals for research and education cannot be easily eliminated outright. This is partly because animal experimentation is often intended to identify ways to reduce harm to animals. For example, the effective development of mammal trapping devices used by researchers and trappers involves the implementation of stepwise protocols to minimise pain and suffering and ensures a thorough assessment of traps with a minimum number of animals (Proulx et al., 2012). Without such state-of-the-art research protocols and ongoing refinement of techniques (e.g. Meek et al., 2021), traps used in the field may cause otherwise avoidable pain, suffering and death to millions of animals (Proulx et al., 2020).

Humans do not need to kill animals for research and education purposes, but refraining from this endeavour will undermine our ability to improve animal welfare and minimise animal killing in the future. For example, the animal welfare impacts of agricultural killing practices (Section 2.3) may not improve if we cease researching ways to reduce harm to killed animals, or the harms associated with threatened species conservation efforts (Section 2.6) may not improve if we cease researching ways to increase reintroduction success. In the absence of a universal ethic for animal experimentation, concerned scientists and non-scientists alike have plotted different courses of action while recognising that animal researchers have a role to play as moral stewards of their research animal subjects (Gauthier and Griffin, 2005). Many medical schools have eliminated their live-animal labs or have reduced the number of healthy animals used for surgical practice and experimental procedures. Alternatives to the use of live or dead animals, such as interactive 3D computer models, video footage, and life-size plastic models, can be as effective as traditional methods in some cases (Bishop and Nolen, 2001; Li et al., 2018). In contemporary contexts, the scientific community and the public need to integrate

critical thinking with the scientific method to continually identify necessary and unnecessary animal-based studies (Proulx, 2004), which is presently achieved and managed through various national codes of practice (e.g. SABS, 2008; NHMRC, 2013). Animal researchers and educators must also ensure that published research involving animals meets the highest standards for the use and treatment of animals (Field et al., 2019).

3. Animal killing behaviour in context

We have classified multiple reasons for animal killing behaviour by humans into 10 categories: (1) wild harvest or food acquisition, (2) human health and safety, (3) agriculture and aquaculture, (4) urbanisation and industrialisation, (5) invasive or overabundant animal control, (6) threatened species conservation, (7) recreation, sport or entertainment, (8) mercy or compassion, (9) cultural and religious practice, and (10) research, education and testing. In ecological terms, these animal killing behaviours might be better understood as human expression of interspecific forms of predation, interference competition, exploitative competition, self-defence, optimal foraging, or territoriality or territorial defence – behaviours ultimately intended to improve the prospects for food acquisition or to protect and enhance life. These are innate life objectives for any sentient animal, and each individual, group, population or species (including humans) strives towards these objectives as valuable parts of one enormous, global food web reliant on animal killing to maintain some form of dynamic equilibrium amongst its component parts (Barbosa and Castellanos, 2005; Krebs, 2008; Molles, 2012; Smith and Smith, 2015).

Since 1789, when Antoine Lavoisier discovered that 'mass is neither created nor destroyed, only changed' (Sterner et al., 2011), humans have been cognizant that every living organism ultimately must obtain its essential nutrients from other living organisms. This *First Law of Thermodynamics* or *Law of the Conservation of Mass* underpins what ecologists call nutrient cycling (Molles, 2012). Therefore, maintenance of all life on earth requires obtaining, utilizing, disposing of and recycling chemical elements, and ecosystems can be thought of as a 'battleground' for these elements (sensu Sterner et al., 2011). Each plant and animal also has particular elemental demands that are a unique, relatively fixed, elemental formula or composition determined by its form and function, and failure to meet these elemental demands leads to poor health and welfare, limited reproduction, and eventually death and extinction (e.g. Moen et al., 1999). In other words, avoidance of death requires the death of something else, either through direct (e.g. predation) or indirect (e.g. competition) means.

Some have argued that directly killing animals is unacceptable or that adopting certain herbivorous or no-killing (sensu Hall and Tolhurst, 2007; Wills, 2019) lifestyles or diets (i.e. veganism) can eliminate or greatly reduce animal killing (Singer, 1975; Regan, 1983; Francione, 2009). But achieving a no-killing lifestyle is a physical and ecological impossibility because *all* lifestyles are dependent on multiple forms of accidental or purposeful, indirect or direct, animal killing. For instance, most vegetable and leguminous foods come from crops that are grown on land where animals have been killed or displaced during or have died subsequent to agricultural intervention (Hampton et al., 2021; Section 2.3). Because one cannot kill that which has already been killed, a contemporary no-killing lifestyle might be more accurately termed a post-killing lifestyle. Moreover, while an animal-free diet for humans might temporarily reduce the number of animals that need killing (Singer, 1975), it will only do so until the food demand of growing human populations exceeds the production capacity of farmed arable land. When that point is inevitably reached, humans will have to directly and/or indirectly kill animals again or risk dying themselves, or substantially change their way of life (e.g. to avoid urbanisation and industrialisation; Section 2.4). Regardless, a no-killing lifestyle knowingly results in consumption of food products that indirectly require continued widespread killing of animals in diverse ways (Hall and Tolhurst, 2007; Lecerf, 2020). Humans also need space to live, however small or large that space may be (Section 2.4), which also results in animal killing. The inescapable *Law of the Conservation of Mass* means that the very existence or presence of humans (and every other species) is dependent on the proceeds of killing animals now or in the past (Sterner et al., 2011); humans cannot live independent of this global food web. A contemporary no-killing lifestyle merely emphasises 'humans as competitors' (indirect killing) over 'humans as predators' (direct killing; Fig. 1), but it cannot avoid the necessity of animal killing. For those concerned about animal lives, a more modest position of minimizing animal killing will still involve intentional and unintentional forms of animal killing (Hampton et al., 2021).

These ecological realities further imply that the admonition to 'do no harm' as a means of obtaining 'peaceful coexistence' with animals (Wallach et al., 2018) is demonstrably impossible (e.g. Hayward et al., 2019; Johnson et al., 2019; Callen et al., 2020; Hampton et al., 2021). Thus, eliminating all forms of direct and indirect animal killing by humans will ultimately be fruitless given the fundamental biophysical laws that demand such animal killing to support continued life on Earth (Sterner et al., 2011; Molles, 2012; Smith and Smith, 2015). 'Coexistence' is a term often and mistakenly used to infer, imply or encourage abstinence from animal killing (e.g. Dorresteijn et al., 2016; Morehouse et al., 2018; Bogezi et al., 2019; Hartel et al., 2019; Hunold and Mazuchowski, 2020; Treves and Santiago-Ávila, 2020; van Eeden et al., 2021), but this is ecologically inaccurate. Coexistence *requires* killing and death; coexistence *is not* the absence of animal killing or death (Gravel et al., 2011; Chapron and López-Bao, 2016; Hart et al., 2017; Pooley et al., 2021). If this were not the case, then even the slow-breeding African elephant *Loxodonta africana* would overrun the whole Earth within a short time, as described in Charles Darwin's 'elephant problem' (Darwin, 1859; but see also Podani et al., 2018). In the words of D.P. Roberts (1987), "life is pain [and] anyone who says differently is selling something". As the only known animals with an ethical or moral conscience, humans have the ability and responsibility to assume a managerial, caretaker or stewardship role over all other animals, to resolve negative interactions between them as best as possible, or to optimize welfare for as many individual animals as possible (Lewis et al., 2017). However, this will still require killing some animals to benefit others, including ourselves, as part of a dynamic process that occurs over large spatial and temporal scales.

4. Conclusions

Killing animals occurs in multiple ways for multiple reasons and, although some forms of killing are not essential for human existence (e.g. recreational hunting, mercy killing), the overall necessity of animal killing is an unavoidable ecological reality. We caution, however, that current levels of animal killing are unsustainable in many cases and must be modified somehow. Human populations have increased to such a degree that we now require animal killing on enormous scales to feed ourselves (Sections 2.1 and 2.3), house ourselves (Section 2.4), protect ourselves (Sections 2.2, 2.5, and 2.10), and contribute to the diversity of our ways of life (Sections 2.6–2.9; see also Crist et al., 2017). Satisfaction of the *Law of the Conservation of Mass* may require animals to die, but it does not require humans to live. So if human populations continue to grow at the rates we are growing without changing our food consumption practices or material way of life, then not only will animal populations crash (Ripple et al., 2014, 2015, 2016), but human populations will ultimately crash as well (Erlich, 1978). For "just as the constraints of mass balance provide a useful tool for ecologists in studying natural ecosystems, mass balance also ensures that the increase in human population and material consumption that has characterized the past 200 years cannot continue indefinitely" (Sterner et al., 2011). Growth cannot be infinite on a finite planet.

Direct and indirect forms of animal killing are an ecological necessity and will undoubtedly remain an ongoing human endeavour, as it will likewise remain for non-human animals. Animal killing by humans is also a behaviour consistent with our predatory and competitive ecological roles within the global food web. We acknowledge, however, that these arguments only get us to the point of demonstrating that animals must die and that some of those will be intentionally killed – these arguments do not necessarily sanction direct human participation in all forms of animal killing. This requires additional ethical arguments beyond the

ecological arguments we have described here, arguments that benefit from an acknowledgement of the distinction between animal ethics and animal welfare, and between human rights and human welfare. We further acknowledge that others may identify additional or complementary reasons for human animal-killing behaviour, and we invite others to build on the discussion we have initiated here. A constructive dialogue that (1) accepts human participation in one enormous global food web dependent on animal killing and (2) focusses on the nuances of animal welfare and sustainability, instead of killing or not killing, is likely to improve the lives of animals to a greater extent than vain efforts to vilify human animal-killing behaviour altogether. We hope to see such constructive dialogue and encourage respectful comment and further discussion.

Article impact statement

Killing animals is a necessary component of our inescapable involvement in a single, functioning, finite, global food web.

CRediT authorship contribution statement

BA conceptualised the review and contributed the initial shortlist of topics discussed. Thereafter, all authors contributed equally to the development of the concepts, design, authorship and editing of the manuscript.

Data accessibility statement

All data associated with this article is available and contained within the article.

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Data availability

No data was used for the research described in the article.

Declaration of competing interest

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